BULLETIN OF MARINE SCIENCE, 55(1): 176–192, 1994 CORAL REEF PAPER

THE TROPICAL WESTERN ATLANTIC PEROPHORIDAE (ASCIDIACEA): I. THE GENUS *PEROPHORA*

Ivan Goodbody

ABSTRACT

Five species in the genus *Perophora* occur in the tropical western Atlantic, distinguished by morphology and habitat requirements. *P. viridis* and *P. regina* have four rows of stigmata and longitudinally oriented mantle muscles; *P. multiclathrata, P. bermudensis* and *P. carpenteria* n. sp. have five rows of stigmata and transversely oriented mantle muscles. Specific differences in the arrangement of the mantle muscles are considered to be of taxonomic importance. *P. bermudensis* is considered to be a valid species and not a synonym of *P. multiclathrata.* In the absence of a designated Type an original specimen of *P. bermudensis* from the type locality is declared to be the Neotype. *P. viridis* is the most cosmopolitan of Caribbean species while *P. regina* and *P. bermudensis* are restricted to areas of fairly strong flowing currents in mangrove channels. *P. multiclathrata* is characteristic of quiet sheltered environments and *P. carpenteria* flourishes in shallow water with moderately agitated water flow.

The family Perophoridae is primarily a warm water group of ascidians although a few species, notably in the genus *Perophora,* penetrate into temperate and high latitudes. The characteristic feature of the family is a system of stolons from which individual zooids arise at intervals to form colonies consisting of either clusters of zooids (e.g., *Ecteinascidia turbinata* Herdman, 1880), creeping mats in which the individual zooids in the colony are more widely spaced (e.g., *Perophora viridis* Verrill, 1871) or erect branching colonies in *Perophora namei* Hartmeyer and Michaelsen, 1928 from the Pacific. Unlike some other colonial ascidians (e.g., *Polyclinum, Eudistoma*) the zooids of the Perophoridae are always separate from one another and only connected by the system of stolons. This paper is the first in an intended series which examines the taxonomy and biology of the tropical western Atlantic species in the family.

The family contains only two genera, *Perophora* Wiegmann, 1835 and *Ecteinascidia* Herdman, 1880. In general the zooids of *Ecteinascidia* are larger than those of *Perophora* but overlap in size occurs. The distinction between the two genera (Fig. 1) is based primarily on the number of rows of stigmata in the branchial sac, the organization of the alimentary canal and the form of the testis (Kott, 1985). Most *Perophora* species have only four or five rows of stigmata, but one Pacific species *Perophora multistigmata* Kott, 1952 is exceptional in having eight rows. In those cases where five rows of stigmata occur some stigmata span the width of rows one and two indicating that the additional row is split off from the original first row and hence four is the primary number of rows. In *Ecteinascidia* there are always more than eight rows of stigmata and usually between twelve and twenty. In *Perophora* the gut loop is horizontal and the rectum short; *Ecteinascidia* has a more open curved gut loop and a long rectum. The testis in *Ecteinascidia* usually forms an open crescent of pyriform lobes arranged inside the loop of the gut and discharging by a series of ducts to a single sperm duct or vas deferens. In *Perophora* the testis seldom has more than four lobes, often only one, situated in the gut loop.

Mantle musculature has received little attention as a character of importance in ascidian taxonomy in spite of the fact that it has considerable functional significance. Branchial pressure is controlled by the activity of the siphons and the

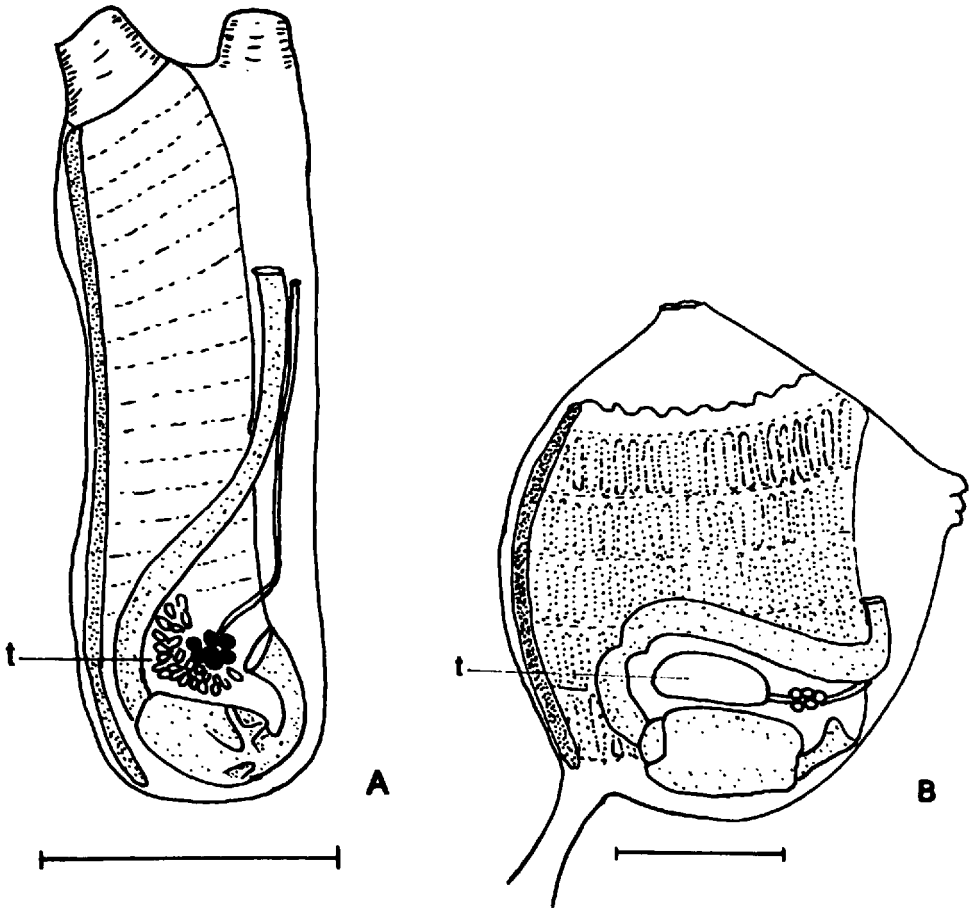

Figure 1. Comparison of typical *Ecteinascidia* (*E. turbinata* Herdman) [A] with *Perophora* (*P. bermudensis* Berrill) [B] showing the more open gut loop, larger number of rows of stigmata and large number of pyriform testis lobes in *Ecteinascidia*. For clarity the mantle musculature is not shown. Scale A: 0.5 cm, B: 1.0 mm.

mantle musculature (Goodbody and Trueman, 1969; Goodbody, 1974) and hence feeding activity must also be influenced by these muscles. Although taxonomic significance is probably more important at the species, than the generic, level it is to be noted that in *Ecteinascidia* there are usually broad areas of transverse fibers on the mantle, particularly in the anterior end, while the arrangement of fibers in *Perophora* is usually more discrete and involves fewer fibers. This is discussed further below.

This paper deals exclusively with the species of *Perophora* occurring in the tropical western Atlantic, viz: *Perophora viridis* Verrill, 1871, *Perophora regina* Goodbody and Cole, 1987, *Perophora bermudensis* Berrill, 1932, *Perophora multiclathrata* (Sluiter, 1904) and *Perophora carpenteria* n. sp. These five species belong to two distinct groups characterized by the number of rows of stigmata and the arrangement of mantle musculature. *P. viridis* and *P. regina* have only four rows of stigmata and the mantle musculature is primarily of longitudinal origin. The remaining three species have five rows of stigmata, the most anterior row being confluent with the second so that some stigmata extend through both

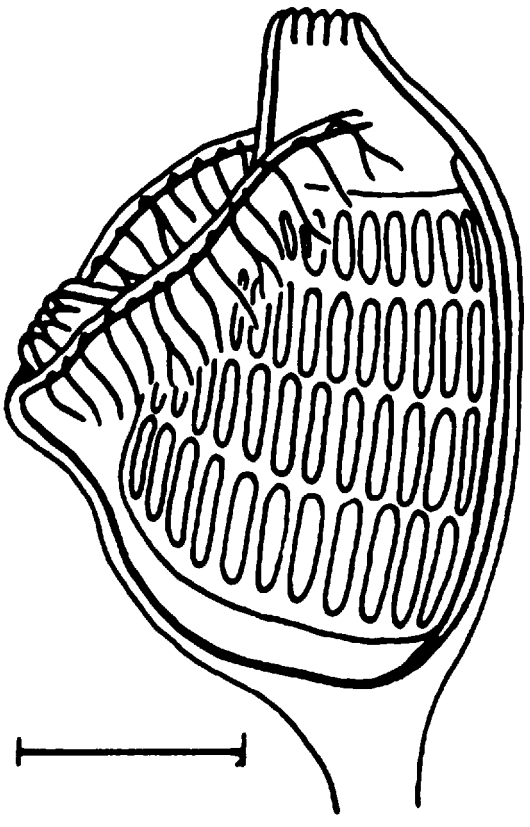

Figure 2. The arrangement of mantle musculature in *Perophora viridis* (from Goodbody and Cole, 1987). Scale 1.0 mm.

rows; these species have mantle musculature which is primarily of transverse origin imparting a circular type contraction to the body.

In recent taxonomic literature *P. bermudensis* has been treated as a synonym of *P. formosana* (Oka, 1931) (Monniot, 1983) which is itself now considered a synonym of *P. multiclathrata* (Nishikawa, 1984; Kott, 1985). In this paper it will be shown that *P. bermudensis* is quite distinct from *P. multiclathrata* not only in morphology but also in its ecology; the morphological distinctiveness was clearly recognized by Arnback-Christie-Linde (1935) (see below).

Material

The material on which this paper is based has been collected in Jamaica, Belize, Bermuda, Bonaire and Puerto Rico. This has been supplemented by examination of additional museum material as follows: a colony of *P. bermudensis* collected by Berrill in 1932 (Rijksmuseum, Stockholm, #1537); a syntype of *P. formosana* Oka, 1931 (Imperial Household, Tokyo, #27); Sluiter's type specimen of *P. multiclathrata* (Zoological Museum, Amsterdam, TU 558-4); a specimen of *P. multiclathrata* from Puerto Rico collected by P. Wagenaar Hummelinck in 1963 (ZMA, TU 1640); several specimens of *P. multiclathrata* from Lac of Bonaire, Netherlands Antilles, collected by P. Wagenaar Hummelinck in 1967 (ZMA, TU 2049; TU 4020) and specimens of *P. multiclathrata* from the collections of the Queensland Museum representing material from Wistari Reef, Queensland (QH 4272), Heron Island (GH 3819), Norfolk Island (QH 4678), Fiji (G 12468) and the Philippine Islands (GH 444).

Perophora viridis Verrill, 1871
Figure 2

Perophora viridis Verrill, 1871 p. 359.
Perophora viridis Van Name, 1945 p. 165.

Although many authors make reference to *Perophora viridis* there are few comprehensive accounts and only that of Van Name (1945) is in any way complete. The account which follows amplifies and modifies Van Name's description.

The test is thin and transparent and the zooid frequently looks green; this is due to blood cells circulating in the underlying mantle and is not a function of the test. One of the most characteristic features of *P. viridis* which distinguishes it from other Caribbean members of the genus, but allies it closely with the European *Perophora listeri* Forbes and Hanly, 1848, is the arrangement of the mantle musculature. On each side of the zooid there are about 12 short longitudinal muscles arising anteriorly and extending about one quarter the length of the zooid. These muscles have their origin from an anastomosis of fibers arising on the two siphons and on an oval area of tissue between the siphons, referred to by Goodbody and Cole (1987) as the siphonal plate. The action of these muscles on contraction is such as to pull in the anterior end of the zooid like a diaphragm and to pull the siphons down into the now depressed siphonal plate. Small circular muscles occur on the siphons but nowhere else.

The branchial sac has four rows of stigmata usually with only 17 or 18 stigmata per row, the most dorsal of which is often reduced in size. Van Name (1945) reported over 20 stigmata per row which is probably a function of slightly larger zooids in colder North American waters. On the internal face of the branchial sac small papillae arise from the transverse vessels running between the rows of stigmata, usually eight on each vessel so that there are two stigmata between each papilla. The papillae arise from a membranous triangular base and some, but not all, bifurcate to give longitudinal processes anteriorly and posteriorly but these seldom unite to form internal longitudinal vessels. In general the most anterior transverse vessel has the best developed papillae and the posterior vessel may have no such development. In those cases where longitudinal processes develop, a small extension of the papilla inwards into the branchial sac forms a secondary papilla as has been described in *P. regina* by Goodbody and Cole (1987). The dorsal lamina is a thin membrane from which three languets hang down into the branchial sac, one level with each of the transverse vessels. The opening of the neural gland appears as a simple oval aperture.

Both the branchial and atrial siphons have six or more prominent pointed lobes and there are normally 20 branchial tentacles, 10 large and 10 small, but this number may vary and the small tentacles may sometimes be rudimentary.

The horizontal gut loop, situated on the left side, is simple and has a small rounded stomach and usually a bilobed anus. In the living animal, there is a lot of orange pigment in the stomach wall, a feature apparently peculiar to *P. viridis* and distinguishing it from other Caribbean members of the genus.

The gonads are situated in the gut loop. The male gonad usually consists of four pear-shaped follicles, the vasa efferentia of which unite to form a single sperm duct opening just posterior to the anus. The ovary, which develops later than the testis, is situated close to the proximal end of the sperm duct. A short and very thin oviduct extends as far as the posterior end of the dorsal lamina where it crosses the dorsal side of the branchial sac and discharges into a brood pouch formed in the posterior right side of the atrial cavity; the pouch does not develop until the eggs are ready to discharge. This arrangement of the female

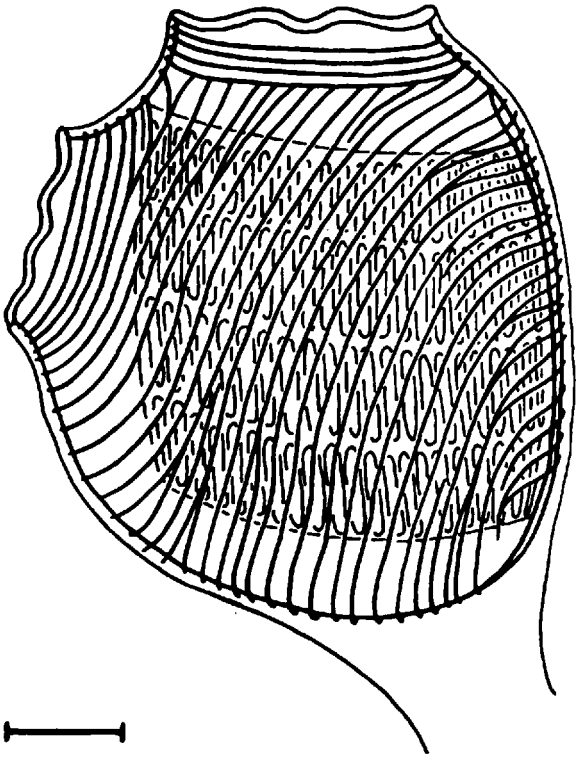

Figure 3. The arrangement of mantle musculature in *Perophora regina* (from Goodbody and Cole, 1987). Scale 1.0 mm.

reproductive system is common to all members of the genus *Perophora* (Mukai et al., 1983; Goodbody and Cole, 1987).[1]

In the Caribbean, *P. viridis* grows abundantly in inshore lagoons and relatively quiet, productive bodies of water. The creeping stolons run like vines over the surfaces of hard substrata such as mangrove roots, oysters or other sessile organisms; they particularly favor the bryozoan *Amathia vidovici* (Heller) and less frequently *Zoobotryon verticillatum* (Delle Chiajei); the perophorid stolon runs along the stem of the bryozoan so that a complete intermingling of the two organisms occurs. Ovoid zooids arise from the stolonic base at regular intervals; they are sessile on the stolon and not, as implied by Van Name (1945) borne on the tips of the branches, or as in some other species of *Perophora,* on a short stalk or pedicel.

Perophora regina Goodbody and Cole, 1987
Figure 3
Perophora regina Goodbody and Cole, 1987 p. 246

Colonies of *P. regina* have a dense basal stolonic network creeping over the substratum, from which the zooids arise on short stalks. In mature colonies the zooids are tightly packed so that the colony as a whole presents a smooth outline.

[1] Contrary to the view expressed by Kott (1985) it is this author's opinion that the brood pouch is not a morphological component of the oviduct but develops independently. This will be discussed further in a later paper on perophorid reproduction.

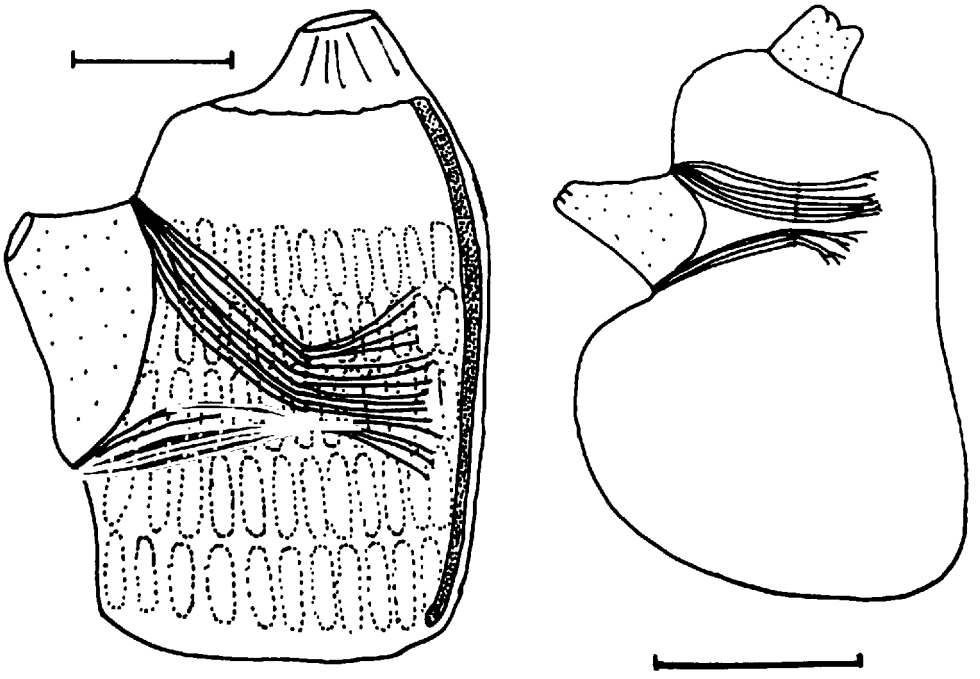

Figure 4. The arrangement of mantle musculature in *Perophora multiclathrata*. (left) Fully expanded zooid. (right) Contracted zooid. Scale 0.5 mm.

The zooids of *P. regina* are characterized by their large size (4 to 6 mm), prominent white pigment spot on either side of a yellow neural gland situated between the siphons, four rows of large stigmata and powerful obliquely placed longitudinal mantle musculature. The testis contains 12 to 15 separate lobes each discharging to a common sperm duct, and the ovary, as is normal for the genus, is situated just posterior to the base of the sperm duct. Also, like other members of the genus, *P. regina* broods its embryos in a brood pouch on the posterior right side of the atrial cavity. In keeping with its larger size *P. regina* lays about twice as many eggs as do smaller species in the genus; this will be discussed in a later paper.

A complete description of *Perophora regina* has recently been published (Goodbody and Cole, 1987) and the reader is referred to this for further detail.

At the time of writing, *P. regina* is known only from a few localities on the Barrier Reef in Belize, Central America. It grows profusely on mangrove roots in channels where water flow is relatively fast and it appears to be intolerant of stress from temperature or salinity extremes.

Perophora multiclathrata (Sluiter, 1904)
Figure 4 and Plate 1

Ecteinascidia multiclathrata Sluiter, 1904 p. 12.
Perophora multiclathrata Nishikawa, 1984 p. 123.
Ecteinascidia formosana Oka, 1931 p. 173.
Perophora formosana Tokioka, 1953 p. 218.
Perophora formosana C. Monniot, 1983 p. 57.
Perophora orientalis Arnback-Christie-Linde, 1935 p. 6.
Perophora africana Millar, 1953b p. 304.

This is one of the three species in the genus *Perophora* which occur in the Caribbean and which have five (not four) rows of stigmata in the branchial sac. This condition apparently arises during development by the splitting of the anterior of the original four rows; in most cases some long stigmata occur which are not divided and hence extend through the first and second rows.

The zooids are small, 2.0 to 2.5 mm in length and are sessile (or with very short stalks) arising from a creeping stolon; this sessile habit distinguishes the species immediately from *P. bermudensis* and *P. carpenteria.* The short stalks reported by some authors (Kott, 1985) apparently are an extension of the zooidal test and not true stolonic pedicels as occur in *P. bermudensis* (Plate 1). The distinctive mantle musculature consists of a bundle of fibers on either side crossing the mantle wall near the middle, arising just dorsal to the endostyle and drawn together at a nodal area in the center of the mantle wall; from this node fibers radiate dorsally so as to provide two fibers crossing the dorsal side at a node just anterior to the atrial siphon, and another array of fibers, usually three, crossing the dorsal side immediately posterior to the atrial siphon. The anterior and posterior fibers are linked by a prominent circular fiber surrounding the base of the atrial siphon. The action of these muscles is quite distinctive, it causes pouching (or an inward movement) of the lateral wall as described by Goodbody and Cole (1987) and pulls the entire atrial siphon uniformly inward, a movement quite distinct from that of *P. bermudensis* (cf. below). This arrangement of muscles is beautifully displayed in one of the zooids of the type specimen.

The branchial sac has 15 to 20 stigmata per row and in Pacific specimens (Nishikawa, 1986) a corresponding number (or slightly less) of internal longitudinal vessels supported on short papillae arising from the transverse vessels. In Jamaican specimens the papillae are usually mere buttons and internal longitudinal vessels are absent or reduced to one or two incomplete bars crossing the anterior rows of stigmata. In specimens from the Lac of Bonaire prominent papillae occur on the transverse vessels but internal longitudinal vessels are not complete and are represented only by small outgrowths from the papillae. In the Puerto Rico specimen from Bahia Fosforescente there are 20 stigmata per row, prominent papillae but only eight internal longitudinal vessels concentrated toward the ventral side. Regional variability in the number of stigmata in a row and the number of internal longitudinal vessels is also recorded for specimens collected in the Pacific (Nishikawa, 1986). The dorsal lamina is a plain membrane with four short languets, one at each junction with the transverse vessels of the branchial sac. These languets are apparently derived from branchial papillae and are normally arranged along the left side of the lamina. The prepharyngeal groove[2] is not a simple ring but is slightly crenulated giving it a lobed appearance; functionally this arrangement extends the length of the groove (cf. *P. bermudensis* below). The opening of the neural gland is an oval slit and there are normally about twenty branchial tentacles of two different sizes alternating with one another; however, some specimens appear to have as few as twelve tentacles.

The horizontal gut loop is simple and conforms to the arrangement generally found in the genus. The stomach, however, is elongate, not rounded, and has a prominent groove along its length.

The large testis is an undivided pear- to kidney-shaped mass and the sperm

[2] In this paper I have followed Kott's (1985) terminology to identify the groove around the anterior limits of the perforated part of the pharynx as the *prepharyngeal groove.* Earlier authors (e.g., Brien, 1948; Berrill, 1950; Millar, 1953a; Goodbody, 1974) have referred to this structure as the *peripharyngeal groove.* Kott's terminology is appropriate to the anterior location of the groove between the perforated pharynx and the unperforated prebranchial area behind the ring of tentacles. Peripharyngeal suggests a structure outside of or surrounding the pharynx as in the case of the peribranchial cavity (=atrial cavity).

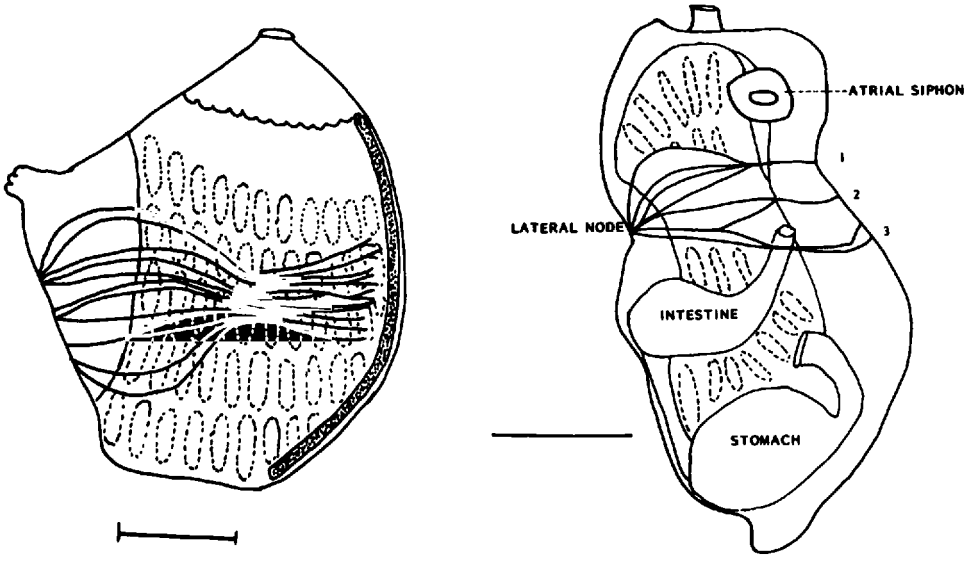

Figure 5. The arrangement of mantle musculature in *Perophora bermudensis*. (left) Fully extended zooid. (right) Dorso-lateral view of a contracted zooid. Scale 0.5 mm.

duct normally arises from a central, not terminal, position. The ovary, as is typical for the genus, develops just posterior to the base of the sperm duct and eggs are discharged through a thin-walled oviduct into a brood pouch at the posterior right side of the atrial cavity.

In the Caribbean, *P. multiclathrata* occurs as small colonies under stones on reefs (e.g., Carrie Bow Cay and Pelican Cays in Belize; Hunter's Bay in Bermuda) or in quiet sheltered situations in mangrove or other lagoons (e.g., lagoons at Port Royal and Salt Marsh in Jamaica; Lac of Bonaire in Netherlands Antilles; Bahia Fosforescente in Puerto Rico). The type specimen was collected in shallow water on a reef at Nusa Island, north east of East Timor in the Banda Sea, Station 234 of the Siboga Expedition (Sluiter, 1904; ZMA #TU-558-4). The species is apparently widely distributed in the Indo-Pacific (Kott, 1985) and may be widely distributed elsewhere (cf. Discussion at the end of this paper).

Perophora bermudensis Berrill, 1932
Figure 5 and Plate 1

Perophora bermudensis Berrill, 1932, p. 78.
Perophora bermudensis Arnback-Christie-Linde, 1935 p. 6.
Perophora bermudensis Van Name, 1945 p. 167.
Perophora fasciata C. Monniot, 1991 p. 500.

Perophora bermudensis was described from Bermuda in a very brief report (Berrill, 1932) which recognized only the fact that it has five, not four, rows of stigmata. Berrill (pers. comm.) has confirmed that he did not designate a type specimen and I have been unable to locate living specimens in Bermuda during visits in May and August 1991. However Berrill sent specimens to Arnback-Christie-Linde at the Rijksmuseum in Stockholm. Arnback (1935) wrote a very concise comparison between Berrill's *P. bermudensis* and specimens of a *Perophora* from Misaki in Japan which she attributed to a new species *Perophora or-*

ientalis which is clearly synonymous with *P. multiclathrata* (Kott, 1985). The subtle but functionally important distinctions described by Arnback have been overlooked in recent works (C. Monniot, 1983; Nishikawa, 1984; Kott, 1985) which synonymize *P. bermudensis* with what we now recognize as *P. multiclathrata.* It is my opinion that on morphological and ecological grounds these two species are distinct and that *P. bermudensis* should be retained as a valid species.

The zooids of *P. bermudensis* are slightly larger than those of *P. multiclathrata,* usually about 3.0 mm in length and while there may be aggregation of green pigment around the siphons the zooid is generally transparent and lacking in color. Colony form may take one or other of two forms. The basal stolonic mass may run long distances through the surface of the mangrove peat bank and zooids rise individually from this on long thread like pedicels which may in some cases exceed 5 mm in length. (Thirteen pedicels ranged from 1.7 mm to 6.0 mm with a mean of 3.7 mm $\pm$ 1.5.) In such cases the observer sees isolated zooids at intervals along the substrate. When growing on hanging mangrove roots, or similar structures, a tangled array of stolons forms a dangling mass, sometimes half a meter or more in depth, and zooids arise all through this, each one mounted on a separate pedicel. Dangling masses of this sort usually hang in the path of a water current. The colony collected by Berrill and now in the Rijksmuseum in Stockholm is of this dangling form. The long pedicels probably have functional significance in providing flexibility in the face of changing current patterns, enabling the zooid to change its position in relation to water flow (Kott, 1989). This flexibility is not available to the sessile type of zooid found in *P. viridis* and *P. multiclathrata.* The creeping stolons of *P. bermudensis* are often brown in color and rigid as if they were mildly chitinized on the outside, a condition not seen in any of the specimens of *P. multiclathrata* examined by me.

The zooid of *P. bermudensis* is also functionally different from that of *P. multiclathrata* through a slight, but significant, re-arrangement of the mantle musculature. The fibers have their origin centrally just above the level of the endostyle and are constricted into a conspicuous lateral node; dorsal to this node the fibers initially fan out and then all of them turn posteriorly uniting to form a small number of fibers crossing the dorsal mantle wall posterior to the atrial siphon and uniting with similar fibers from the other side of the zooid. There are no muscle fibers crossing the dorsal side anterior to the atrial siphon and the prominent ring muscle seen in *P. multiclathrata* is absent so that strong contraction in this species results in pouching of the lateral mantle wall and bending of the atrial siphon toward the posterior of the zooid. Functionally this is quite a different arrangement from that found in *P. multiclathrata* where the siphon is uniformly pulled down in a transverse direction.

The branchial sac of *P. bermudensis* is well developed, often with 20 to 25 stigmata per row and usually 12 papillae on each transverse vessel. The papillae support complete internal longitudinal vessels crossing stigmata rows two, three and four with tentacle like bars extending freely anteriorly over row one and posteriorly over row five. The dorsal lamina is a flat strap with tentacle like languets at the level of each transverse branchial vessel as in other members of the genus. There are usually 20 branchial tentacles of two sizes alternating with one another, and the prepharyngeal groove is more prominently crenulated than in *P. multiclathrata*; this latter feature is probably only a function of size but markedly extends the length of the groove.

The alimentary canal is similar to that of *P. multiclathrata* with an elongate stomach and prominent typhlosole. The undivided testis is elongate oval and the sperm duct arises from the dorsal end of the testis (Arnback, 1935). The ovary

and oviduct are typical of the genus and in sexually active zooids a brood pouch develops on the right posterior side of the atrial cavity.

It is this author's opinion that the differences between *Perophora multiclathrata* and *Perophora bermudensis* are sufficiently constant and distinct to warrant retaining them as distinct species, in which case the specimen of *Perophora bermudensis* housed at the Rijksmuseum in Stockholm and collected by Berrill in 1932 should now be declared the Neotype of this species. The specimen is No. 1537 in the collection of that museum.[3]

Perophora bermudensis occurs abundantly in parts of the mangrove system at Port Royal, Jamaica and at Twin Cays on the Barrier Reef in Belize. In both localities it is characteristic of places where strong currents of water flow through narrow channels or along the edges of the peat bank.

Although hitherto *Perophora bermudensis* has appeared to be exclusively a Caribbean species Monniot (1991) has recently described a species from New Caledonia which he named *Perophora fasciata* but which is clearly identical with *P. bermudensis* as described in this paper, thus extending the range of the species to the Indo-Pacific. Monniot's figures show a normal arrangement of five rows of stigmata, transverse mantle muscles passing only posterior to the atrial siphon and a heavily crenulated prepharyngeal groove. Although not illustrated he describes the arrangement of zooids mounted on pedicels ("petite tige") exactly as in *P. bermudensis*. Monniot's specimens were collected at about fifteen meters in Noumea but no other environmental data are provided.

Perophora carpenteria new species
Figure 6 and Plate 1

Perophora carpenteria is characterized by the small size of the zooids (ca. 2.0 mm), arising on short pedicels from a diffuse meshwork of stolons, five rows of stigmata and a diffuse mantle musculature which encircles the body crossing both in front of and behind the atrial siphon and crossing below the endostyle.

Individual zooids are usually bright green, particularly around the siphons but also on the mantle, due to an abundance of pigment granules and pigmented blood cells in the mantle wall. The branchial siphon is anterior and has six pointed lobes; the atrial siphon, also with six lobes, is situated about one third of the way back along the dorsal side. Zooids in the type specimen vary from 1.8 to 2.0 mm in length and 1.1 to 1.4 mm in dorso-ventral breadth; however, zooids up to 3.00 mm have been identified in one colony.

The arrangement of muscle fibers in the mantle wall appears to be variable. In one zooid of the type eleven fibers pass below the endostyle, spaced along the length of the zooid, four fibers join to form a node as they cross the dorsal side anterior to the atrial siphon and four form a node posterior to the atrial siphon. In another zooid only eight fibers cross below the endostyle, five converge anterior to the atrial siphon and four posterior to it. Fibers are never gathered into a lateral node on the mantle wall as in *P. multiclathrata* and *P. bermudensis* but there are always fibers crossing the dorsal side anterior and posterior to the atrial siphon and there are always fibers crossing ventrally below the endostyle.

The branchial sac has five rows of stigmata with usually 15 or 16 stigmata per row in rows two and three. There are at least 12 complete internal longitudinal vessels raised on papillae arising from the transverse vessels of the branchial sac;

---

[3] The Neotype is a colony of 40 zooids many of them removed from their surrounding test by earlier researchers; some are partially dissected. There are no sexually mature zooids in the Neotype; mature samples collected by the author in Belize are being deposited in the U.S. National Museum of Natural History.

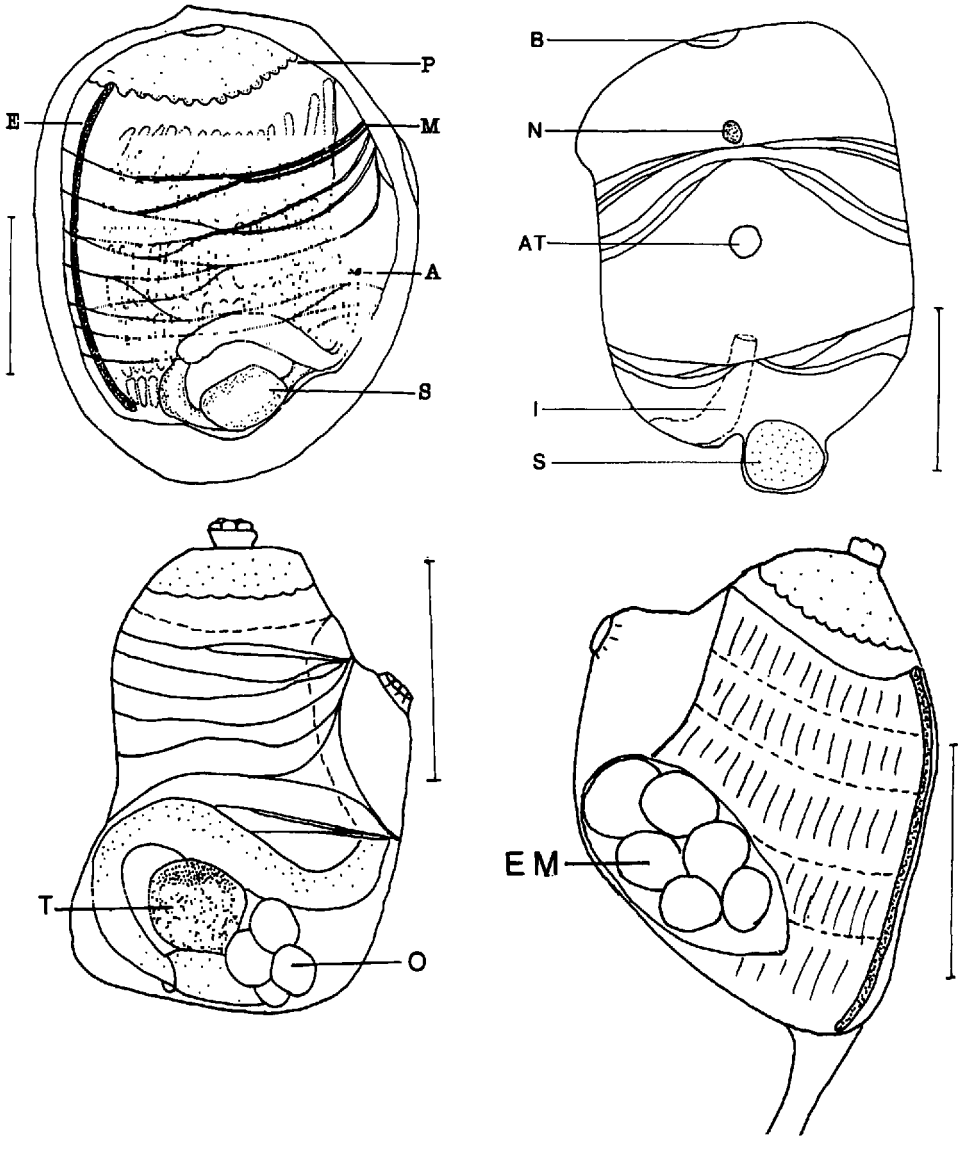

Figure 6. *Perophora carpenteria* n. sp. (upper left) A ventro-lateral view to show manner in which muscle strands encircle the body under the endostyle and converge anterior and posterior to the atrial siphon on the dorsal side. (upper right) A dorsal view of a zooid to show the muscle nodes anterior and posterior to the atrial siphon. (lower left) Left side of a zooid to show the gonads in the loop of the gut. This zooid shows a slightly different arrangement of muscle fibers to that illustrated in (upper left) including a ring nerve around the atrial siphon similar to that found in *P. multiclathrata.* (lower right) Right side of a zooid showing the position of the brood pouch (muscles not shown). *Key*: A: Anus; AT: Atrial siphon; B: Branchial siphon; E: Endostyle; EM: Embryo; I: Intestine; M: Muscle; N: Neural gland and ganglion; O: Ovary; P: Prepharyngeal groove; S: Stomach; T: Testis. Scale 1.0 mm.

there may sometimes be fourteen papillae, the dorsal and ventral papillae not giving rise to internal bars. The lamina is a simple membrane with four tentacular languets on the left side, one at each junction with the transverse vessels. There are approximately 24 branchial tentacles of two sizes irregularly arranged inside

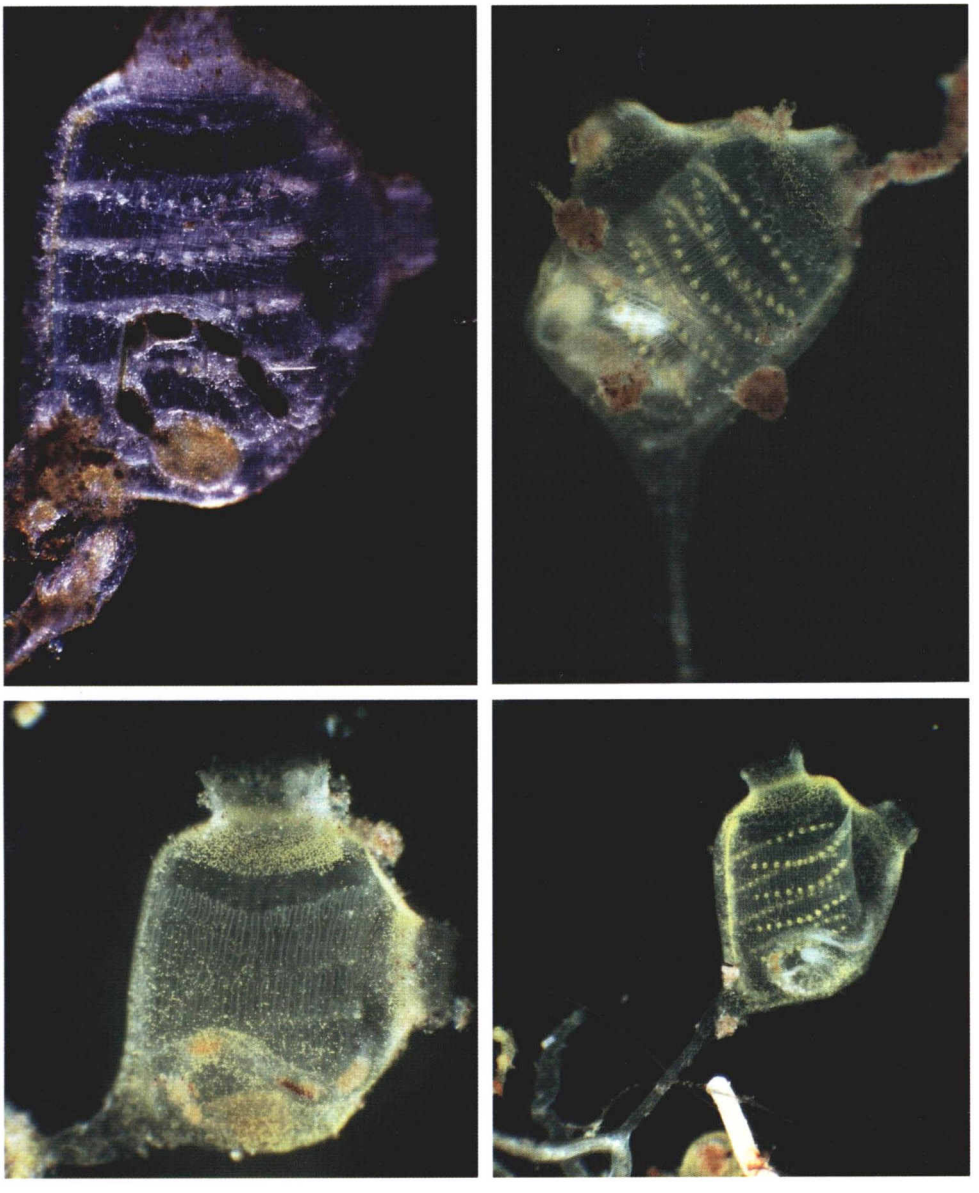

Plate 1. (a) Top Left. Zooid of *Perophora multiclathrata* showing one bundle of muscle fibers running to the anterior of the atrial siphon and another bundle toward the posterior side of the siphon. Coloration is altered through use of filters. (Photo: Peter Parks/Oxford Scientific Films). (b) Top Right. Zooid of *Perophora bermudensis* focussed at the level of the mantle muscle. Note how the muscles draw together at a lateral node (center of field) and then fan out before they all cross to the other side posterior to the atrial siphon. The marked crenulation of the prepharyngeal groove is well illustrated. The cord of faeces in the branchial siphon is aberrant and was sucked in just before the photograph was exposed. (c) Bottom Left. Zooid of *Perophora carpenteria* n. sp. showing the short stalk and five rows of stigmata with some large stigmata (center of field) crossing rows one and two. The prepharyngeal groove is not obviously crenulated. The fine muscle strands encircling the body are not visible at this focal level. (d) Bottom Right. Zooid of *Perophora bermudensis* to show the long pedicel on which the zooid is supported.

the branchial siphon. The prepharyngeal groove is crenulated (about ten lobes on each side) but not so prominently as in *P. bermudensis.*

The alimentary canal is typical for the genus but the stomach is less elongate and more rounded than is found in *P. multiclathrata* or *P. bermudensis* (a typical stomach measures 500 μm long and 300 μm in greatest diameter). The testis is globular to pear-shaped and the sperm duct arises from the dorsal tip. The ovary is normal for the genus placed posterior to the origin of the sperm duct and the thin walled oviduct discharges into a brood pouch at the posterior end of the right side of the peribranchial cavity. As in other members of the genus, brood pouches only develop when the ovaries ripen and are ready to discharge eggs.

The species is named in recognition of Mike Carpenter, Operations Manager for the Smithsonian Institution's Caribbean Coral Reef Ecosystems Program (CCRE) without whose friendship and frequent assistance in the field this work on the Perophoridae would not have been possible.

The Holotype and two Paratypes were collected from near the entrance to Hidden Creek in Twin Cays, Belize, Central America, in approximately 1 m of water. The colonies were growing on blades of the seagrass *Thalassia testudinum* Koenig. Colonies were narcotized in menthol, fixed in formaldehyde and later transferred to alcohol for storage. They are deposited in the National Museum of Natural History, Washington, D.C., and are designated as follows:

Holotype. Colony containing approximately 150 zooids collected 10 May 1990 (U.S.N.M. No. 20026).

Paratypes. (i) About 25 zooids, being portion of a larger colony, collected 25 April 1990 (U.S.N.M.) No. 20027. (ii) Colony of about 150 zooids, detached as three separate clusters, collected 21 May 1989 (U.S.N.M. No. 20028).

The animal is abundant in mangrove channels and lagoons at Twin Cays and other islands in Belize where it grows in very shallow water along the peat bank, on hanging mangrove roots, on blades of Turtle Grass (*Thalassia*) and frequently on various sponges especially the black sponge *Spongia tubulifera.* In general *P. carpenteria* grows in shallower water than *P. bermudensis* and in places where the water current is less strong. This and other aspects of its ecology will be discussed in a later paper. I have also found specimens of *P. carpenteria* at Walsingham Pond and Coney Island Bridge in Bermuda which suggests that it may have a much wider distribution throughout the Caribbean.

Discussion

The information presented in this paper suggests that the genus *Perophora* contains two quite distinct groups which have evolved separately. On the one hand are those which have only four rows of stigmata and in which the mantle musculature is predominantly longitudinal. *Perophora viridis* (cf. this paper), *P. listeri* (Tokioka, 1954; Goodbody and Cole, 1987), *P. clavata* (Kott, 1985), *P. japonica* and *P. sagamiensis* (Tokioka, 1953), all have longitudinal muscles extending only a short way down either side of the zooid, while *P. regina* (Goodbody and Cole, 1987), *P. modificata* and *P. namei* (Kott, 1985) have longitudinal muscles extending the length of the zooid. On the other hand, are those species which have five rows of stigmata and in which the mantle musculature is primarily transverse. This second group includes *P. multiclathrata, P. bermudensis* and *P. carpenteria* as described in this paper and also *P. hutchinsoni* (Kott, 1985). *P. multistigmata* (Kott, 1985), which has eight rows of stigmata, appears to have predominantly transverse musculature.

Perophora regina (Goodbody and Cole, 1987) and *P. viridis* (this paper) have

Table 1. Morphological characteristics of three closely related species: *Perophora multiclathrata, P. bermudensis* and *P. carpenteria*

P. multiclathrata	*P. bermudensis*	*P. carpenteria*
Zooids sessile or on very short stalks	Zooids on long pedicels arising from stolonic base	Zooids on short pedicels Never sessile
Zooids 2.0 to 3.0 mm	Zooids 3.0 to 3.5 mm	Zooids 1.0 to 2.0 mm
Mantle muscles converge to a node on lateral wall	Mantle muscles converge to a node on lateral wall	Mantle muscles widely spaced and do not form node; circle body ventral to endostyle
Muscles converge anterior and posterior to atrial siphon	Muscles converge posterior to atrial siphon only	Muscles converge anterior and posterior to atrial siphon
Prepharyngeal groove slightly crenulated	Prepharyngeal groove strongly crenulated	Prepharyngeal groove slightly crenulated
Spermduct normally arises from middle of testis	Spermduct arises from dorsal end of testis	Spermduct arises from dorsal end of testis

been found to have secondary branchial papillae. It would be interesting to know if this condition exists in other species with four rows of stigmata and longitudinal musculature.

Although the Caribbean species with five rows of stigmata must be closely related, the differences between them are sufficiently constant and striking to warrant maintaining their rank as separate species. The distinction between *P. multiclathrata* and *P. bermudensis* is perfectly clear and was described almost 60 years ago by Arnback-Christie-Linde (1935). *P. carpenteria* is quite distinct from either species, although probably more closely related to *P. multiclathrata* than to *P. bermudensis.* The morphological differences between these three species relate to colony structure, zooid size, mantle musculature, and to a lesser extent the form of the prepharyngeal groove and the origin of the sperm duct. The principal differences are summarized in Table 1.

While morphological characters provide the primary distinction between different species of *Perophora* they are also distinguished on ecological grounds. *P. viridis* is probably the most cosmopolitan of Caribbean species and is essentially a primary colonizer. In the mangrove channels and lagoons of Twin Cays, Belize and Port Royal, Jamaica, it frequently occupies and quickly covers new space such as the growing tips of *Rhizophora* roots, recently bared roots, oyster shells or artificial substrates such as panels, bottles, etc., placed in the water. While it seems to show a preference for substrates hanging clear of the peat bank it is not confined to such sites and may occur on bank-side roots. Nevertheless, it flourishes on substrates at the mangrove fringe where sediment loading is minimal, and in such places may develop large colonies on the stems of the bryozoan *Amathia vidovici. P. regina,* on the other hand, is very conservative in its habitat requirements confined to fast flowing water such as occurs in Hidden Creek at Twin Cays, Belize. It has a marked preference for the distal portions of hanging *Rhizophora* roots, often completely clothing 20 cm or more of the tip of the root, and in most cases on roots which are hanging well clear of the adjacent peat bank. Nevertheless, colonies will occasionally grow over the surface of certain sponges, particularly species of *Haliclona,* but these do not develop into the tightly packed colonies found on root tips. *P. regina* is clearly sensitive to thermal and salinity stress and in some mangrove channels its distribution is controlled by these factors.

In the Caribbean *Perophora multiclathrata* seems to require relatively quiet water with good but not rapid water circulation such as occurs under stones on

back reef flats and in mangrove lagoons at Port Royal, Jamaica, Mayaguez, Puerto Rico and the Lac of Bonaire. *P. bermudensis*, on the other hand, frequents areas of the mangrove environment where water currents at times are rapid; examples of this environment and in which *P. bermudensis* occurs are to be found at Twin Cays, Belize (Hidden Creek and entrance to the Lair) and in Jamaica at the entrance channel to the Port Royal mangroves and in similar channels near the entrance to West Harbour, Clarendon. The Neotype of *P. bermudensis* has no collecting locality attached to it other than it was collected in Bermuda but in a recent letter (June 1991) to Wolfgang Sterrer at the Bermuda Museum, Berrill indicates that it probably came from under boulders along the causeway at the lower water level. The bridge structure [at that time] was a ramshackle affair and has since been replaced with a modern structure. My own failure to find *P. bermudensis* in Bermuda in 1991 may not be due to inadequate searching. Bermuda is probably at the northern limits of the range of *P. bermudensis*. In the period between 1932 and 1991 two major changes have occurred. The causeway has been rebuilt and a new bridge constructed, and during 1941–1943 massive dredging and reclamation to build the airport took place in adjacent Castle Harbour. Dodge and Vaisnys (1977) have produced evidence to show that the process of dredging created conditions of sedimentation which produced mass coral mortality in Castle Harbour. These same conditions may have created so much suspended sediment as to kill off many ascidians, perhaps including *P. bermudensis*. If this is correct it may be that there has been no opportunity for re-colonization of this species which has fairly specialized ecological requirements. Specimens collected by Monniot (1972) are all *P. multiclathrata* (Monniot, 1983; C. Monniot (pers. comm.).

Perophora carpenteria seems to replace *P. multiclathrata* in the mangrove environment of the Barrier Reef in Belize, although it seems more tolerant of strong water movement than is *P. multiclathrata*. It occurs in shallow water all through the mangrove system particularly in areas of intermediate water flow close to and on the peat bank, and on the leaves of *Thalassia testudinum*.

The ecological requirements of Caribbean species of *Perophora* and changes in their populations over time will be discussed in a later paper.

Of the five species of *Perophora* considered in this paper, two (*P. regina* and *P. carpenteria*) are at present known only from the western Atlantic. *Perophora viridis* appears to be primarily a species of the western Atlantic ranging from Cape Cod to Surinam (Van Name, 1945; Millar, 1978; Monniot, 1972, 1983; Goodbody, 1984) but it has also been recorded from the Mediterranean (for references see Monniot and Monniot, 1987a) and in the Pacific from Tahiti (Monniot and Monniot, 1987b) and New Caledonia (Monniot, 1987). The appearance of *P. viridis* in New Caledonia is surprising given the fact that extensive previous collecting in the western Pacific has not revealed its presence elsewhere in that region.

P. multiclathrata appears to be widespread throughout the tropics both in the Pacific and Atlantic (see for instance Kott, 1985, 1992; Monniot, 1987; Monniot and Monniot, 1987a; this paper). On the other hand, the distribution of *P. bermudensis*, both regionally and globally, remains problematic. It is certain that confusion has taken place between *P. bermudensis* and *P. multiclathrata* in assigning Caribbean specimens of perophorids with five rows of stigmata and extensive new collecting or a review of all museum specimens will have to take place before the distribution of *P. bermudensis* in the western Atlantic is clarified. Outside of the western Atlantic the specimen collected in Noumea by Monniot

(1991) and named by him as *Perophora fasciata* is the only apparent record of *Perophora bermudensis.*

ACKNOWLEDGMENTS

I am grateful to the Smithsonian Institution and in particular K. Ruetzler for supporting my work in Belize and making it possible for me to use the facilities at Carrie Bow Cay. I am also grateful to M. Carpenter for assistance in Belize and to W. Sterrer for re-introducing me to Bermuda and its marine habitats. I thank P. Mather for reading a first draft of the manuscript; the final paper has benefitted greatly from her critical comments, and also those of C. Monniot and S. de Almeida Rodriques. I thank UNESCO and the Netherlands Universities Foundation for International Cooperation (NUFFIC) for supporting a visit to the Zoological Museum in Amsterdam and Professor S. Van Der Spoel for providing me with facilities at the Instituut Voor Taxonomische Zoologie. I also thank Oxford Scientific Films Limited for permission to reproduce Peter Parks' photograph of *Perophora multiclathrata* (Plate 1b). This is Contribution Number 389, Caribbean Coral Reef Ecosystem Programme, Smithsonian Institution, partly funded by a grant from the Exxon Corporation.

LITERATURE CITED

Arnback-Christie-Linde. 1935. A notable case of relation in *Perophora.* Arkiv. F. Zool. 28B No. 9, 1–6.

Berrill, N. J. 1932. Ascidians of the Bermudas. Biol. Bull. 62: 77–88.

———. 1950. The Tunicata. Ray Soc. Publs. 133: 1–354.

Brien, P. 1948. Embranchement des Tuniciers. Pages 553–930 *in* P. Grassé, ed. Traité de Zoologie Tome XI (C). Masson, Paris.

Dodge, R. E. and J. M. Vaisnys. 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. J. Mar. Res. 35: 715–730.

Forbes, E. and S. C. T. Hanly. 1848. A history of British Molluscs and their shells, Vol. 1, p. 28. London.

Goodbody, I. 1974. Ascidian physiology. Pages 1–149 *in* F. S. Russell and C. M. Yonge, eds. Advances in marine biology, Vol. 12.

———. 1984. The ascidian fauna of two contrasting lagoons in the Netherlands Antilles: Piscadera Baai, Curacao and the Lac of Bonaire. Stud. Fauna Curacao Carib. Isl. 67: 21–61.

——— and L. Cole. 1987. A new species of *Perophora* (Ascidiacea) from the Western Atlantic, including muscle action in related species. Bull. Mar. Sci. 40: 246–254.

——— and E. R. Trueman. 1969. Observations on the hydraulics of *Ascidia.* Nature, London 224: 85–86.

Hartmeyer, R. and W. Michaelsen. 1928. Ascidiae Diktyobranchiae und Ptychobranchiae. Fauna Sudwest—Aust. 5: 251–460.

Herdman, W. A. 1880. Preliminary report on the Tunicata of the Challenger expedition. Pt. I. Ascidiacea. Proc. Roy. Soc. Edinburgh 10: 458–472.

Kott, P. 1952. Ascidians of Australia. I. Stolidobranchiata and Phlebobranchiata. Aust. J. Mar. Freshw. Res. 3: 206–333.

———. 1985. The Australian Ascidiacea I. Mem. Queensl. Mus. 23: 1–438.

———. 1989. Form and function in the Ascidiacea. Bull. Mar. Sci. 45: 253–276.

———. 1992. The Australian Ascidiacea. Supplement 2. Mem. Queensl. Mus. 32: 621–655.

Millar, R. H. 1953a. *Ciona.* L.M.B.C. Mem. Typ. Br. Mar Pl. Anim. 35: 1–123.

———. 1953b. On a collection of ascidians from the Gold Coast. Proc. Zool. Soc. London 123: 277–325.

———. 1978. Ascidians from the Guyana Shelf. Netherl. J. Sea Res. 12: 99–106.

Monniot, C. 1972. Ascidies phlébobranches des Bermudes. Bull. Mus. Natn. Hist. Nat. Paris 3 Sér. No. 82, Zool. 61: 939–948.

———. 1983. Ascidies littorales de Guadeloupe II. Phlébobranches. Bull. Mus. Natn. Hist. Nat. Paris 4 Sér., 5, A (1): 51–71.

———. 1987. Ascidies de Nouvelle-Calédonie I. Phlébobranches du lagon. Bull. Mus. Natn. Hist. Nat. Paris 4 Sér., 9, A (1): 3–31.

———. 1991. Ascidies de Nouvelle-Calédonie VIII. Phlébobranches. Bull. Mus. Natn. Hist. Nat. Paris 4 Sér., 12, A. Nos. 3–4, 491–515.

——— and F. Monniot. 1987a. Discussion sur la valeur de deux genres d'Ascidies à propos d'espèces nouvelles en Méditerranée. Ann. l'Inst. Océanog., Nouv. Sér. 63: 119–130.

——— and ———. 1987b. Les Ascides de Polynésie francaise. Mem. Mus. Natn. Hist. Nat., Paris, Zool., 136: 143 pp. 5 pl.

Mukai, H., H. Koyama and H. Watanabe. 1983. Studies on the reproduction of three species of *Perophora* (Ascidiacea). Biol. Bull. 164: 251–266.

Nishikawa, T. 1984. Ascidians from the Truk Islands, Ponape Island and Majuro Atoll (Tunicata, Ascidiacea). Proc. Jap. Soc. Syst. Zool., 27: 107–140.

———. 1986. Ascidians from the Gilbert and Solomon Islands and Nauru I. Perophoridae, Ascidiidae and Corellidae. Proc. Jap. Soc. Syst. Zool., No. 32: 30–78.

Oka, A. 1931. Ueber eine neue species von *Ecteinascidia* aus Formosa. Proc. Imp. Acad. Jap. 7: 173–175.

Sluiter, C. P. 1904. Die Tunicaten der Siboga-Expedition. Pt. I, Die socialen und holosomen Ascidien. Siboga Exped. 56A: 1–126.

Tokioka, T. 1953. The ascidians of Sagami Bay. Iwanami Shoten, Tokyo. Pp. 1–313.

———. 1954. Invertebrate fauna of the intertidal zone of the Tokara Islands VII. Ascidians. (Contributions to Japanese ascidian fauna VII.) Publ. Seto Mar. Biol. Lab., III(3): 239–264.

Van Name, W. G. 1945. The North and South American ascidians. Bull. Amer. Mus. Nat. Hist. 84: 1–476.

Verrill, A. E. 1871. On the distribution of marine animals on the southern coast of New England. Amer. J. Sci. Arts (3) II: 357–363.

Wiegmann, Fr. A. 1835. Bericht über die Fortschritte der Zoológie im Jahre 1834. Arch. Naturg. I.I. 3: 309–311.

DATE ACCEPTED: March 31, 1993.

ADDRESS: *Zoology Department, University of the West Indies, P.O. Box 12, Kingston 7, Jamaica, West Indies.*